

MODE OF LIFE OF THE MIDDLE CAMBRIAN ELDONIOID LOPHOPHORATE *ROTADISCUS*

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ABSTRACT. The discs of the alleged 'medusoids' *Rotadiscus* from the recently discovered Mid Cambrian soft-bodied Kaili fauna in South China are commonly overgrown by shelled epizoans of unknown affinities. Most are attached to the convex side of the disc, near its margin. Towards the disc centre only small shells occur usually, which suggests that their growth was inhibited by an anoxic environment under the disc. The eldonioids were thus sedentary animals, analogous to Recent deep-water thecocyathid corals, with the discs passively lying on the mud surface with the convex side of the disc orientated downward.

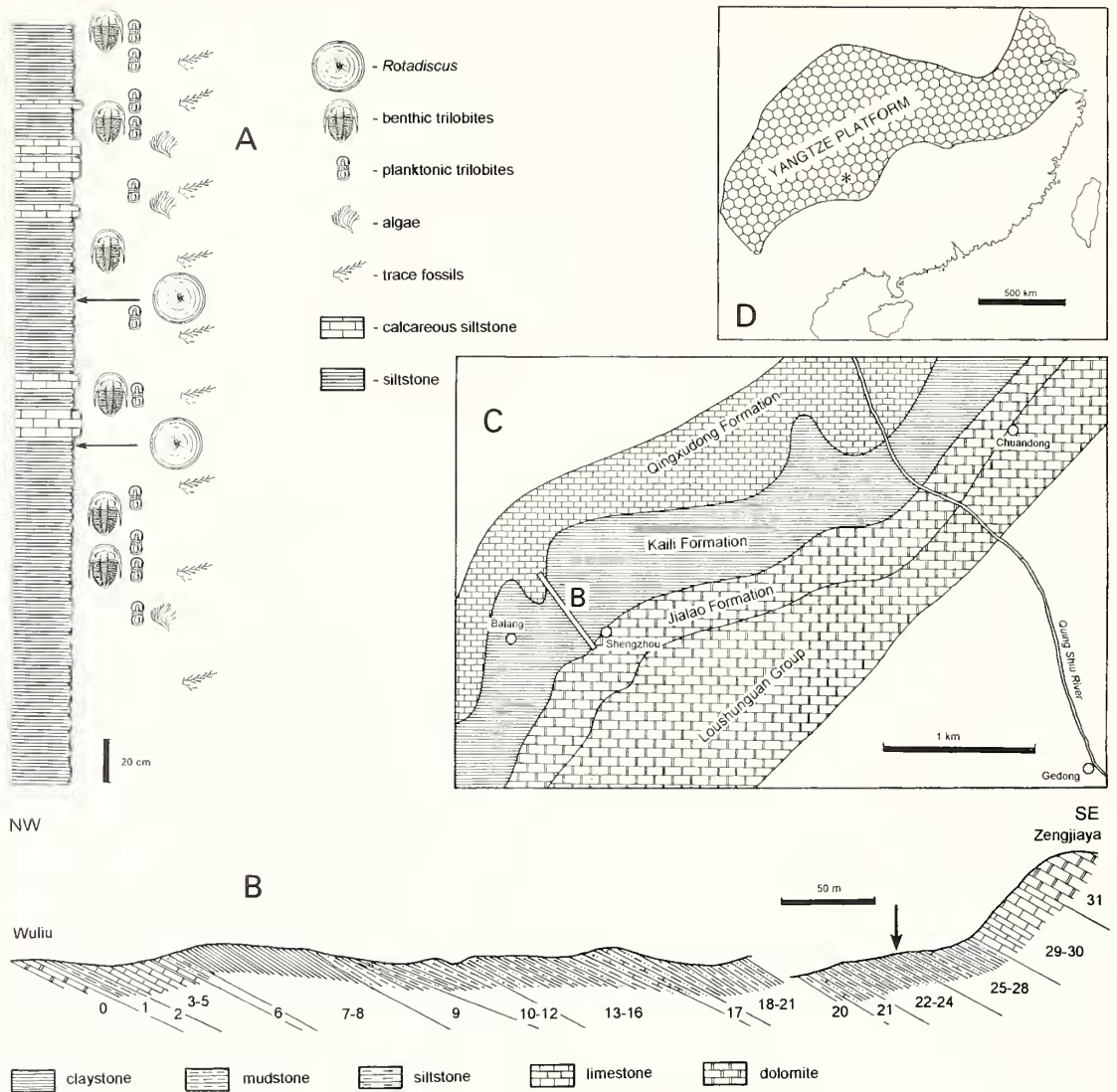
THE assumption that coelenterates, including medusae, are represented among the oldest fossils is questionable for various reasons, both with respect to Cambrian (Dzik 1991) and Vendian (Seilacher 1989) faunas. Moreover, some pyritized fossils from the early Devonian Hünseruck slate of western Germany that were proposed to represent fossil siphonophorans (Stanley 1986), as well as alleged ctenophorans from that locality (Stanley and Stürmer 1983, 1987), are more likely to be poorly preserved shelly or echinoderm fossils (Otto 1994). No convincing evidence is thus available for the presence of medusoid coelenterates prior to the mid Palaeozoic. Some Cambrian fossils, although clearly of non-coelenterate anatomical organization, continue to be called the 'medusoids' of that period, ecological analogues of the Recent scyphozoans (Chen *et al.* 1995*b*; Rigby and Milsom 1996). These are the Eldonioidea (Dzik 1991), Cambrian animals with a U-shaped gut enclosed in a low conical, discoidal body bearing a biramous tentacular apparatus – features shared with some lophophorates and echinoderms. Unlike echinoderms, the eldonioids do not have any mesodermal calcitic skeleton but, instead, a cuticular cover secreted marginally by a kind of mantle (Dzik 1991). In some cases this external skeleton, bearing distinct growth lines, was stiff enough to be preserved in coarse sandstones, originating as mass flow sediments (Masiak and Żylińska 1994).

In this paper we provide additional evidence to that presented by Dzik (1991) for the sedentary mode of life of the eldonioids. This is offered by new data on a *Rotadiscus* species occurring abundantly in the Mid Cambrian Kaili fauna (Zhu and Zhao 1995) in Guizhou Province, China. Several hundred *Rotadiscus* specimens (mostly incomplete) have now been collected; about one-third of them are overgrown with epibionts.

The studied specimens are stored at the Department of Geology of the Guizhou Institute of Technology in Guiyang (abbreviated GTB) and the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (ZPAL).

GEOLOGICAL SETTING

Rotadiscus is most common within bed 24 in the upper part of the Kaili Formation. This unit is about 23 metres thick and the eldonioid-rich horizons occur in proximity to the first calcareous mudstone bed in the formation (Text-fig. 1), the type of rock that characterizes the overlying bed 25 and higher units. The strata are rich in articulated pelagic and benthic trilobites and other excellently preserved fossils. These include abundant uncalcified algal thalli and rare isolated *Wiwaxia* sclerites. The mudstone is regularly laminated, without bioturbation or preserved infaunal organisms. The general lack of bioturbation suggests low-oxygen conditions near the sediment–water interface. Skeletal-concentration layers of disarticulated trilobite carapaces do not show any



TEXT-FIG. 1. Location of the fossil site of *Rotadiscus guizhouensis* Zhao and Zhu, 1994 above the village Balang near Taijiang in Guizhou province of China. A, rock column of the most fossiliferous part of bed 24 of the Kaili Formation at this site. B, section along the exposure with the most fossiliferous site arrowed. C, geological map of the area showing distribution of the Kaili Formation and adjacent lithological units, position of the section B indicated. D, map showing location of Yangtze Platform.

features of transportation, preferential orientation or sorting (Zhu and Zhao 1995). There are only a few bedding surfaces on which the trace fossil *Treptichmus* and lingulide brachiopods occur. Some *Rotadiscus*-covered bedding planes occur about 6 m below the first carbonate beds in the uppermost part of the formation (Zhu and Zhao 1995).

Two horizons with mass occurrences of the *Rotadiscus* discs are clearly sedimentary discontinuity surfaces. Similar surfaces are also known in this part of the section with numerous articulated

eocrinoids (*Gogia*). In the latter case, the orientation of the echinoderm tests shows that they were killed instantaneously by a turbiditic flow of sediment, with a basal layer, a few millimetres thick, of coarser mud showing grain gradation (Zhu and Zhao 1995). The fate of the *Rotadiscus* associations was similar, although they are usually covered by a finer sediment. The silty mudstone beds deposited above other such surfaces, usually less than 20 mm thick, may show unidirectional current marks at the basal surface that indicate rapid sedimentation (Zhu and Zhao 1995, p. 8). The original orientation of well-preserved discs scattered over the sedimentary discontinuity surfaces within bed 24, whenever observed in the field, was convex side down.

Yuan *et al.* (1995) correlated the uppermost part of the Kaili Formation, containing the pelagic eodiscid *Peronopsis majiangensis*, with the North American *Plagiura-Kochaspis* Zone, that is with the lowest Middle Cambrian. The Kaili Formation is thus significantly older than the Burgess Shale, being closer in age to the Polish occurrences of eldonioids, in the first Baltic trilobite zone (*Eccaparadoxides insularis*) of the Middle Cambrian (Masiak and Żylińska 1994).

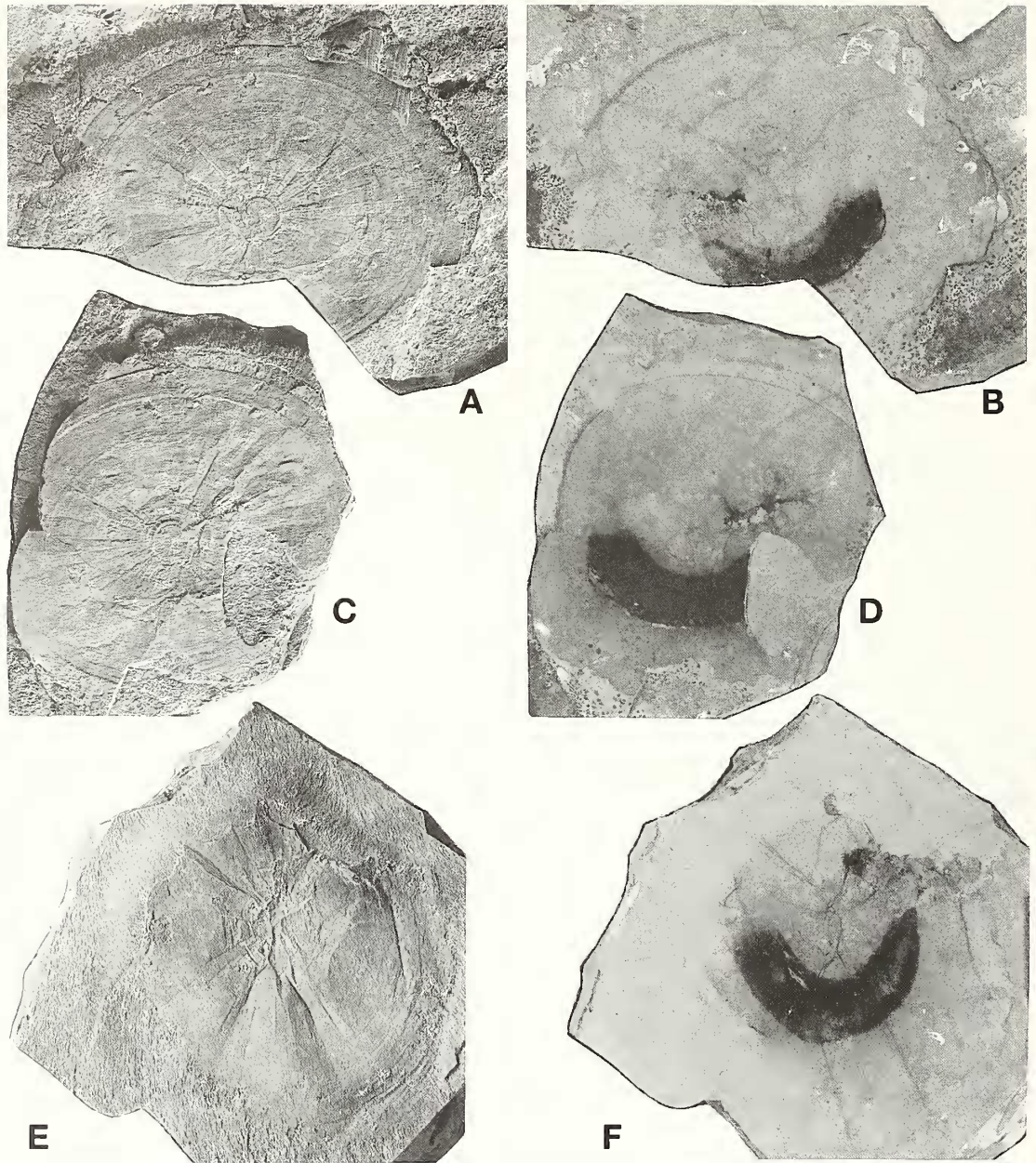
ANATOMY OF *ROTADISCUS*

The Kaili specimens of *Rotadiscus guizhouensis* Zhao and Zhu, 1994 commonly show presumed carbonized remains of soft organs, mostly a U-shaped gut. The specimens are flattened and no internal filling with sediment has been observed, with the possible exception of the specimen ZPAL CH.E/5 where there seems to be a thin layer of mudstone between the level with the imprint of the intestine and the disc wall (Text-fig. 2F). Usually the darkest area, corresponding presumably to the muscular wall of the intestine and its organic-rich content, is followed along both sides by a paler zone delimited externally by dark lines (Text-figs 2B, F, 3A). This corresponds to the structure called the coiled sac by Chen *et al.* (1995b), which seems to be at least analogous to the peritoneum. The most important difference in the internal organizations of *R. guizhouensis* in respect to the Chengjiang and Burgess Shale material is that the intestine was significantly shorter in the Kaili species, with oral and anal openings relatively distant to each other, so that the intestine is truly U-shaped. The posterior end of the intestinal structure terminates abruptly in the Kaili material, which seems to indicate that the posterior part of the digestive tract was empty and not well enough muscularized to impart carbon staining. The dark stain in the anterior part of the intestine is increasingly paler towards the mouth, but some of its structures can be traced to where the two sets of tentacles are located at the corners of the mouth opening (Text-fig. 2D).

The preservation of the fossil is not good enough to show details of the lophophore organization, apart from possibly two bunches of tentacles emerging directly from each of the two bases. Some traces of radial canals (or perhaps muscles) are also visible in the Kaili material (Text-fig. 2F). In two specimens a central cavity is recorded by a pale staining.

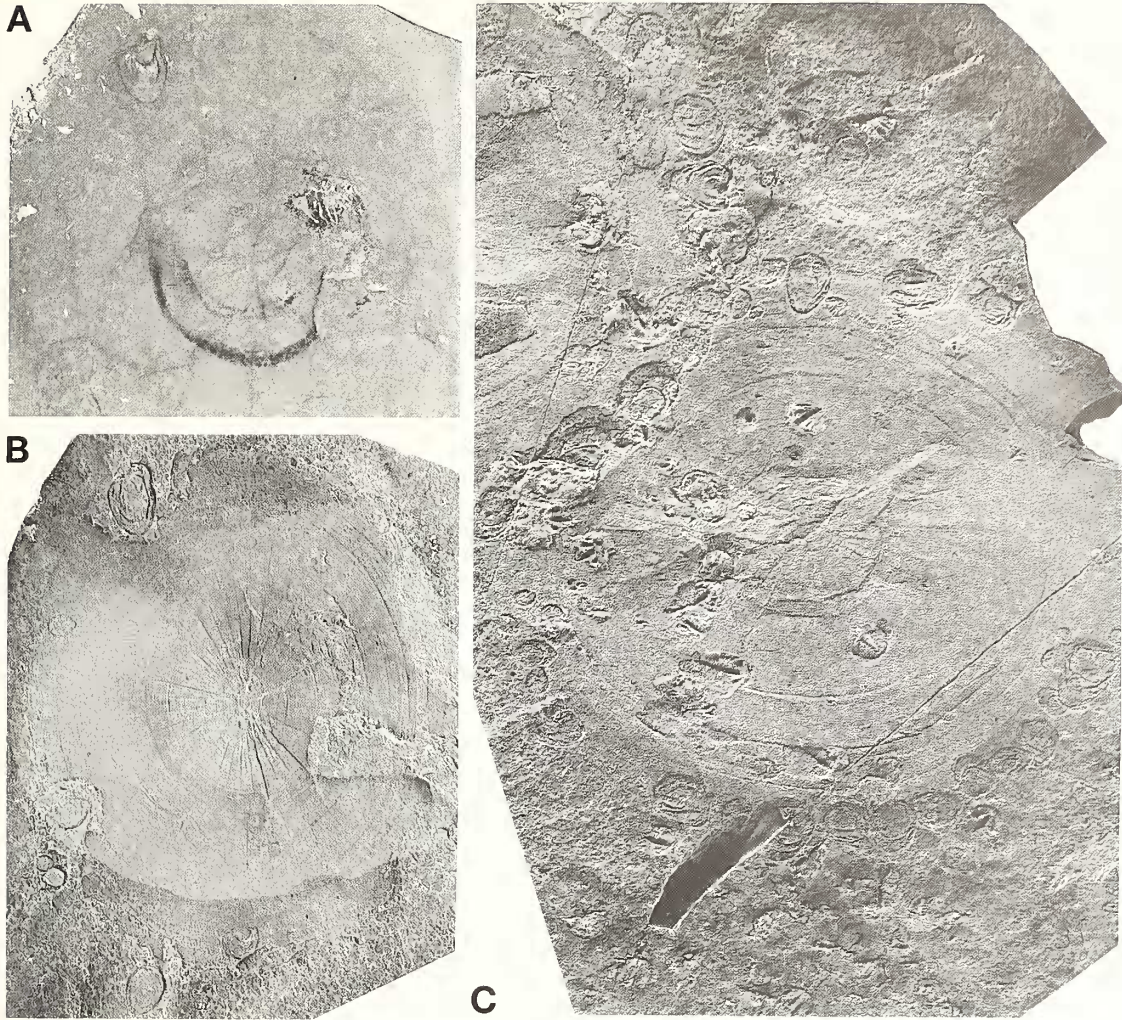
The body of *Rotadiscus* was disc-shaped but not completely flat. Its minimum thickness can be inferred from the diameter of the intestine, which was by no means thin and, together with the peritoneum, corresponds to about one-third of the disc radius (Text-fig. 2E-F). Its dorsal surface was apparently smooth, as no interference of two sets of concentric growth lines systems is observed, as would be the case if the dorsal surface was also sclerotized.

The ontogeny of *Rotadiscus guizhouensis* was more complex than in the ancestral *R. grandis*. The central area of the disc, a couple of millimetres in diameter, seems to be smooth when well preserved (Text-fig. 3C). In numerous cases it bears one or two prominent marginal growth wrinkles (Text-fig. 2A). At this stage, the animal was about 3 mm in diameter. External to these wrinkles, sharp radial furrows develop on the external surface, about 40 in number. They allow easy recognition of the disc side on specimens that are not completely flattened. These furrows make *R. guizhouensis* similar to the coeval Polish *Velumbrella czarnockii* Stasińska, 1960 at this stage of ontogeny, but are almost twice as numerous. The furrows disappear gradually at disc diameters ranging from 20 to 40 mm. The subsequent stage in ontogeny is characterized by a lack of any radial ornament, but the concentric step-like growth lines become more and more prominent and numerous, indicating



TEXT-FIG. 2. *Rotadiscus guizhouensis* Zhao and Zhu, 1994; lower Middle Cambrian, Kaili Formation, Balang; specimens with preserved intestine, photographed whitened with ammonium chloride sublimate (A, C, E) and submerged under alcohol (B, D, F). The oval shape of this and following specimens is an effect of tectonic deformation. A–D, inner and outer side of the disc ZPAL CH.E/3b, a (counterpart and part, respectively). E–F, outer side of the disc ZPAL CH.E/5. All $\times 1.5$.

maturity. The growth of the *Rotadiscus* discs was thus finite, the specimens becoming adult usually at a diameter of about 40 mm, although a specimen with a diameter of 91 mm has been found in bed 24 (the second largest in size, from bed 21, is 69 mm). Only these extremely large specimens



TEXT-FIG. 3. *Rotadiscus guizhouensis* Zhao and Zhu, 1994; lower Middle Cambrian, Kaili Formation, Balang; specimens with epizoans '*Chuandianella*' *subovata* Yuan and Huang, 1994. A–B, outer side of the disc ZPAL CH.E/19 with preserved intestine, photographed submerged under alcohol (A) and whitened with ammonium chloride sublimate (B); note isolated large epizoans and repair of the disc in its lower part. C, part of slab ZPAL CH.E/1 with the sedimentary discontinuity surface covered with discs, which may overlap together with their numerous epizoans; note scattered complete and disarticulated carapaces of the eodiscid *Pagetia*. All $\times 1.5$.

approach the mean sizes of the Chengjiang *Eldonia* and *Rotadiscus*, or the Polish *Velumbrella*. The giant '*Brzechovia*', with its 180 mm diameter discs (Dzik 1991), is significantly larger.

AFFINITIES OF *ROTADISCUS*

The first described species of the group was *Eldonia ludwigi* Walcott, 1911 from the Mid Cambrian Burgess Shale, originally interpreted by Walcott (1911) as a holothurian, a view supported by A. H. Clark (1912, 1913), H. L. Clark (1912) and Durham (1974). According to Madsen (1956, 1957, 1962), *Eldonia* was a siphonophore, whilst Lemche (1960) considered it to be a coelenterate medusa. The specimens of *Eldonia ludwigi*, and even better preserved material of the related *E.*

eumorpha (Sun and Hou, 1987) from the Early Cambrian Chengjiang site, provided anatomical evidence for a more detailed zoological classification of the eldonioids (Dzik 1991; Chen *et al.* 1995b). Another well-known Chengjiang species is *Rotadiscus grandis* Sun and Hou, 1987.

There are no signs of any pentamerous or tetramerous symmetry in the anatomy of *Eldonia*, nor is there any reason to suppose the presence of a mesodermal calcitic skeleton; so both the holothurian and scyphozoan affinities of this animal are difficult to support. A U-shaped intestine (Text-figs 2–3), lophophore, and an ectodermal, marginally accreted skeleton are features of the lophophorates. Such an attribution was proposed for the eldonioids (in the rank of class) by Dzik (1991). The anatomical data on *R. guizhouensis* are consistent with those on the Burgess Shale and Chengjiang species, which shows that the body plan of these organisms was rather uniform. The relatively simple organization of this species, with a strictly U-shaped digestive tract and the disc inferred to be more conical than in other species (Text-fig. 5), may reflect its primitiveness with respect to the larger and more complex eldonioids.

LIMITS OF MOBILITY IN *ROTADISCUS*

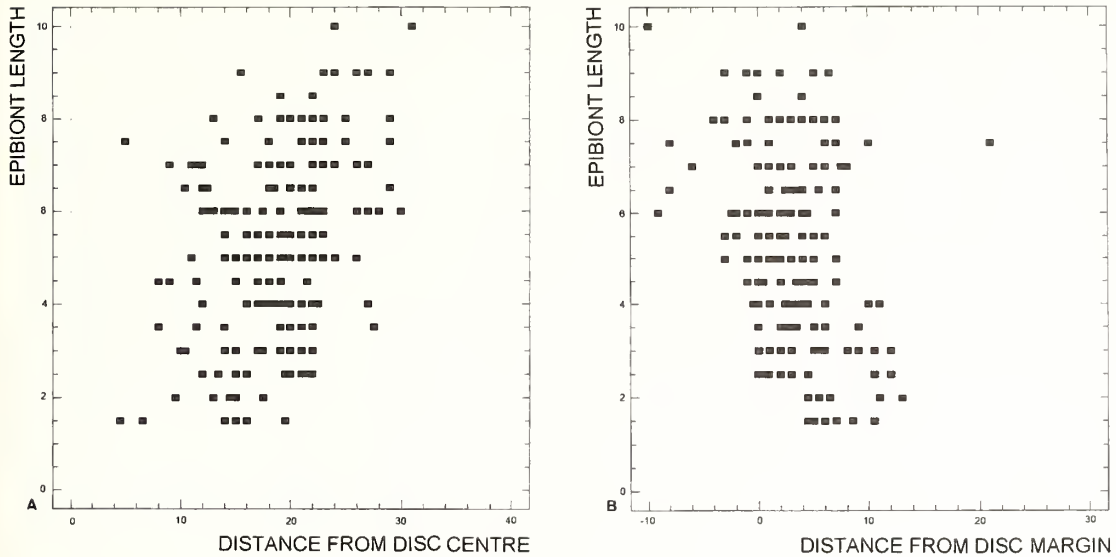
The eldonioids were widespread in Early and Mid Cambrian seas and are known from strata that originated in various environments, ranging from the open marine clays of the Burgess Shale in British Columbia (Walcott 1911) to the coarse sands of the Ocieski Formation in Poland (Stasińska 1960; Dzik 1991; Masiak and Żylińska 1994). Different morphologies are represented in each of these localities; but all three-dimensionally preserved eldonioids show growth lines at least on the convex surface of their discs. In *Eldonia* (Chen *et al.* 1995a, 1995b) the disc was probably only lightly sclerotized, but cuticle accretion was clearly marginal at both ventral and dorsal sides of the body.

The accretional mode of growth implies a certain stiffness of the cuticle and, even if it was not mineralized and thereby flexible in *Eldonia*, its elasticity was definitely low. It is thus unlikely that the circumference of the disc could be reduced significantly by muscle contraction that would enable a medusa-like locomotion. The U-shaped intestine, enveloped in a kind of peritoneum (Chen *et al.* 1995b; see also Text-fig. 3A), implies a coelomate anatomical organization and makes jet propulsion by ejecting water from the gastric cavity equally unlikely. No anatomical structure that could serve as a hydrostatic organ was identified in the excellently preserved Chengjiang specimens. This would be necessary to make the animal buoyant and stable in water with its heavy skeletonized part, lacking any gas-filled chambers, upwards (against the inferred position of the centre of gravity). Thus, a medusoid mode of life cannot be directly inferred from, and seems to be contradicted by, the anatomical organization of *Eldonia*.

There is no particular reason to believe that *Eldonia* was different in this respect from other genera of the Eldonioidea that have basically the same body form, but differ mostly in the degree of sclerotization (and preservation) of their body cover. The stiff skeleton of *Vehumbrella* from Poland fragmented into angular pieces, without any plastic deformation, in a coarse sandstone matrix (Dzik 1991, fig. 3B; Masiak and Żylińska 1994); the Chengjiang *Rotadiscus* 'formed cracks on compaction when compared with wrinkling and folding observed in *Eldonia*' (Chen *et al.* 1995a). In the Kaili species of *Rotadiscus*, repair of the disc skeleton can be observed in rare cases (Text-fig. 3B) – apparently a result of unsuccessful predation of the disc margin. The subsequent regeneration proceeded in the same way as in other marginally secreted shells of molluscs or brachiopods. In Recent pelagic faunas no organism of comparable organization, with strongly sclerotized, marginally accreted skeleton covering only one side of the body, is known. Such skeletal features of the eldonioids are thus hardly compatible with their allegedly 'medusoid' mode of life. The pattern of epibiontic overgrowth of the discs, discussed below, makes this even less likely.

EPIZOANS

Rotadiscus is the most heavily sclerotized eldonioid, although its cuticle was probably not mineralized. In the Kaili Formation, preservation of the *Rotadiscus* disc is different from that of

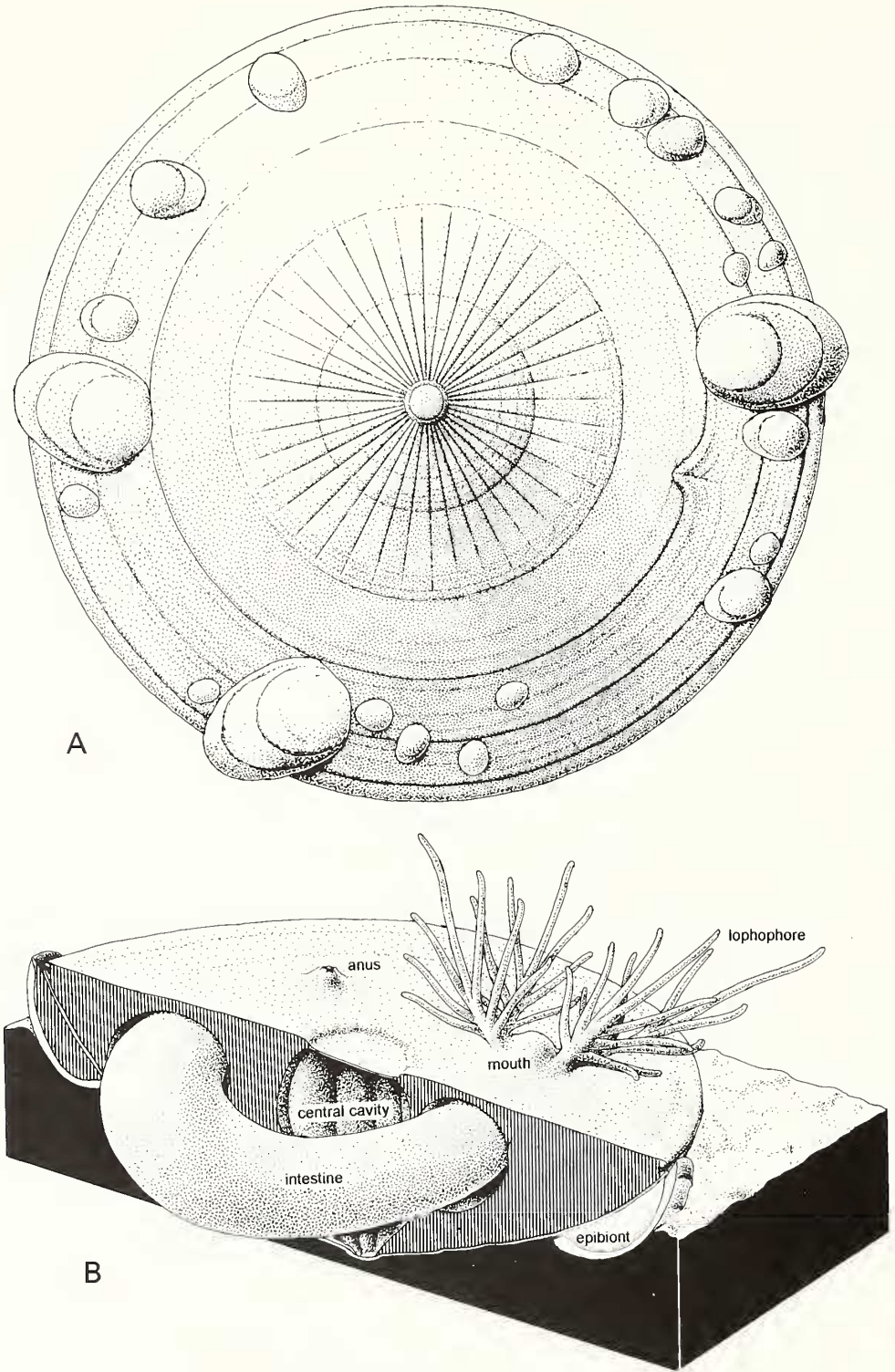


TEXT-FIG. 4. Scattergrams of the epizoans shell length against distance from the centre (A) or margin (B) of the disc of *Rotadiscus guizhouensis* Zhao and Zhu, 1994 from the lower Middle Cambrian Kaili Formation at Balang (based on 22 well-preserved, epibiont-bearing discs from the GTB collection; 36 other discs of comparable preservation from the same collection lack epibionts); incomplete preservation of weakly sclerotized disc margin in some specimens may have resulted in some distortion of the pattern presented by the scattergram B, but note that the shells cluster along the disc margin irrespective of its size.

associated originally calcitic trilobite carapaces and aragonitic mollusc conchs. The discs are always more strongly compressed but, although no breakage or fragmentation has been observed, folds on the disc's surface are always sharply angular and linear. This indicates some rigidity of the skeleton, which was thus, at least potentially, a suitable place for the settlement of epibionts. In fact, filamentous algal thalli radiating from the disc margins in some specimens are suggestive of attachment to its skeletonized surface.

Along with algae, which are usually difficult to discern, more prominent objects do occur in association with the *Rotadiscus* discs in the Kaili Formation. Scattered over the discontinuity surfaces in the upper part of the section, the marginal parts of discs are covered by small oval shells. The zoological affinity of these shells remains obscure. They were originally described as the bradoriid ostracode *Chuandianella? subovata* Yuan and Huang, 1994 and *C.? linguiformis* Yuan and Huang, 1994, although no specimen with two valves in articulation has been found in the Kaili Formation. Virtually all the shells are crushed due to sediment compaction, resulting in the original thickness and outline of the shells being deformed. Only in layers of the mudstone with a slightly higher content of calcium carbonate do they preserve a shape and convexity close to the original (Text-fig. 3B). In such cases the shell outline is ovoid; the shells are bilaterally symmetrical. The rugation, commonly visible on the shell surface, probably represents marginal growth increments. Their arrangement suggests that either at earlier growth stages the shell was more circular and its growth attenuated towards the narrower end of the shell or, more probably, that the shells originally were very convex and their proximal parts are compressed obliquely, resulting in shape distortion. The latter is consistent with small and large epizoans having the same shell outline.

In two specimens (ZPAL CH.E/2 and 13) the epizoans located close to the centre of the disc have their interiors filled with siliceous and clay minerals. The original convexity of the shell is partially preserved. The base remains completely flat, its surface following the rugation of the disc. The



TEXT-FIG. 5. For caption see opposite.

margin of the shell was apparently rather thick – a feature shown also by the empty cavities left after shell margins dissolved in some other specimens. It is thus apparent that the epizoan shells were originally not organic. When compared with *Rotadiscus* discs and associated trilobites, the resistance of the epizoan shells against compaction was intermediate between these two kinds of fossils. The epizoan shells evidently were not calcitic because agnostid carapaces commonly preserve more or less altered original calcareous walls. Perhaps aragonite was involved in the shell construction. Probably in the two better preserved specimens mentioned above, the organic matter of the host *Rotadiscus* protected the aragonite during early diagenesis and only later, after compaction, was it transformed into calcite and replaced by other minerals.

Rarely, some specimens of the epizoan occur disassociated from the *Rotadiscus* discs (for instance, the largest shells in specimen ZPAL CH.E/19; Text-fig 3B). Occasionally such isolated specimens bear prominent ridges that run parallel to each other, without any correspondence to the inferred mode of growth of the shell (see Yuan and Huang 1994, pl. 1, fig. 8). Apparently this is a xenomorphic ornament reproducing rugation of the *Rotadiscus* disc margin. This, together with the already noted flatness and rugation of the basal surface of the epizoans, indicates that the secreting margin of the epizoan shell strictly followed the substrate during growth. Such could be a result of either cementation to the disc surface or at least very strong attachment with a pedicle or byssus.

The shells of the *Rotadiscus* epizoans are always univalved. This refers to those that had apparently fallen from the disc surface, prior to or during the catastrophic covering of the bottom by sediment, but also to specimens still attached to the disc. If they were cemented to the disc, the basal valve must have been very thin and probably inconspicuous.

The bilateral symmetry of the shells, their probable marginal accretion and possibly cementing mode of life, make arthropod affinities of the epizoans seem unlikely. Their shape and inferred mineralogical composition is similar to that of the Early Cambrian inarticulate obolellid brachiopods (see Goryansky and Popov 1985; Geyer 1994) and the monoplacophorans. Similar morphologies and a probable calcareous shell mineralogy also characterize the problematical Cambrian *Apistococoncha*, an organism of possible brachiopod affinities (Bengtson *et al.* 1990). No cementing Cambrian brachiopods are known, however. The only known Mid Cambrian bivalved organism that cemented to the substrate was the operculate coral *Cothonion* (Jell and Jell 1976). Unfortunately, our knowledge of the morphology of the Kaili epizoans, as well as their mode of attachment to *Rotadiscus* discs, frustrates further discussion of their affinities.

PATTERN OF OVERGROWTH

Attachment of the epizoan shells to the *Rotadiscus* discs was rather firm. Discs that happen to overlap always bear their own, clearly identifiable, aureole of marginal shells (Text-fig. 3C). Isolated dispersed shells are rare (a few per cent. of the total number) and their quite occasional occurrence cannot result from their being removed from the central part of the *Rotadiscus* discs. In all the numerous specimens that are not so compressed as to obliterate the relationship of the disc surface to associated objects, they cover the convex surface of the disc. Apparently, the flat surface of *Rotadiscus* was not stiff enough to allow attachment. At least seven epibiont-bearing discs in the studied collection have their internal soft organs preserved (Text-fig. 3A) which proves that *Rotadiscus* was overgrown while alive.

The most puzzling feature of the epibiontic cover of *Rotadiscus* discs is the size distribution of the shells in relation to the disc margin. If the entire surface of *Rotadiscus* was exposed to sea water and the epizoan larvae settled on it randomly, then the largest specimens would be expected close to the

TEXT-FIG. 5. *Rotadiscus guizhouensis* Zhao and Zhu, 1994; lower Middle Cambrian Kaili Formation; restoration of the disc apical surface with attached epizoans '*Chuandianella*' *subovata* Yuan and Huang, 1994 (A) and a disc in its proposed life position sectioned to show the location of the intestine and central cavity (B).

disc centre, that is on its oldest part. In reality, the size-frequency distribution in respect to the disc centre is the opposite; their size being positively correlated with the distance from the disc centre (Text-fig. 4A). Thus, the largest specimens are invariably located at the disc margin. This means that larger discs have generally larger epizoans at their margins, and size-frequency distribution with respect to the distance from the disc margin does not show any apparent pattern (Text-fig. 4B). Small epizoans may thus occur in association with larger ones, but usually in more central positions. Apparently, the epizoans' larvae settled only in proximity to the disc margin where they are concentrated irrespective of the ontogenetic age of the disc (expressed by its diameter; Text-fig 4B). The terminal growth of *Rotadiscus* (evidenced by the condensation of growth lines) suggests that marginal areas of the disc provided longer time spans for the epizoans' settlement than the central areas. Thus, the epizoans crowd close to the margin of mature discs, as if colonization was seasonal, which was probably not the case. Even if the epizoans preferentially settled at the disc margin, their size-frequency distribution cannot be otherwise easily explained if the epibiotic nature of the shells is accepted.

The anatomy of the eldonioids, with their discs covered by a cuticle (thus unable to produce ciliary feeding streams of water) and a centrally located smaller tentacular apparatus (Chen *et al.* 1995b), does not make the disc margin more suitable than the disc centre for life as a filter feeder, assuming that the disc surface was completely exposed to the sea water. The only reasonable explanation for this pattern is that it resulted from a peculiar pattern of epizoan mortality. Rare epizoan larvae that settled on the marginal parts of discs at an earlier stage were subsequently killed by the anoxic conditions under the disc as it lay passively on the black mud. They are relatively uncommon (Text-fig. 4), probably because of the relatively fast growth rate of young discs. The disc margin was a suitable place for epibiont settlement only after its accretion rate decreased and finally ceased with the animal's maturation.

CONCLUSIONS

We propose that the main factor controlling the distribution of the '*Chuandianella*' *subovata* epizoans was the anoxic microenvironment underneath the *Rotadiscus guizhouensis* discs that lay passively on the organic-rich mud. The bottom environment was definitely anoxic during the deposition of the Kaili Formation, as the strata contain abundant articulated pelagic and benthic trilobites and other excellently preserved fossils, with originally non-mineralized skeletons. The rare *Rotadiscus* discs occurring within the parts of the sequence, where a higher sedimentation rate presumably resulted in disc margins not being exposed by winnowing, are commonly devoid of any epibionts. Such is, in fact, the case in the largest known disc (91 mm in diameter).

There are horizons, however, where all the discs bear epibionts. These are bedding planes corresponding to sedimentary breaks. On some of them shoals of *Rotadiscus* developed; other surfaces are covered by numerous gogiid echinoderms. They flourished, with eldonioid disc margins free of sediment cover and encrusted by various epibionts (including filamentous algae, observed in several specimens), until being instantaneously killed by a turbiditic flow of sediment. The type of epibiont growth associated with episodes of lowered sedimentation rate makes it unlikely that the shells (apparently heavy) encrusted the discs as pelagic forms in the water column.

The reasoning presented above remains valid even if one assumes the less likely possibility (contradicted by the xenomorphic ornament and rugated bases in some of the epizoans) that the epizoans were able to change their position on the disc and migrated with the growth of the host disc.

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